Luminous Organs of the Deep-Sea Squaloid Shark, Centroscyllium ritteri Jordan and Fowler

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IN THEIR world-wide revision of the squaloid sharks, Bigelow and Schroeder (1957: 47) referred five species to the genus Centroscyllium, viz.: ritteri, granulatum, fabricii, nigrum, and ornatum. Of these, one species only, C. ritteri Jordan and Fowler, is recorded from the western Pacific region. Since this species appears to inhabit rather great depths, very little regarding it has been reported. Except for the lower dentition, the taxonomic features of Centroscyllium resemble those of Etmopterus, which is known to possess a number of minute luminous organs, particularly in a blackish color pattern. The present study was made in order to determine whether C. ritteri, like the species of Etmopterus, possesses luminous organs.

In regard to the luminous organs of Etmopterus, there is sufficient literature to make an accurate review (e.g., Dahlgren and Kepner, 1908: 134; Ohshima, 1911: 1; Schmidt, 1931: 9). But neither detailed accounts of the luminous organs of *C. ritteri* nor a comparison of them with those of species of the genus Etmopterus have hitherto been presented, though Burckhardt (1900: 567) briefly dealt with the luminous organs in certain species of Centroscyllium. Such a comparison should both extend our knowledge of luminescence in elasmobranch fishes and afford a clearer insight into the nature of their luminous organs.

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MATERIAL AND METHODS

Since *C. ritteri* is relatively rare, only a single specimen measuring 160 mm. from the tip of snout to the origin of upper lobe of caudal fin, and 216 mm. in total length, was available for a dissection. It has been preserved in 10 per cent formalin. The distribution of the luminous organs was first examined by means of a binocular microscope. Then the skin was removed for the microscopic preparations. Sections were made by the usual paraffin method at a standard thickness of 10 μ . The staining methods used were Mayer's hemalum-eosin and Mallory's triple stains.

In order to make a comparison of the luminous organs an embryo of *Etmopterus lucifer* Jordan and Snyder measuring 135 mm. in total length was also sectioned.

OBSERVATIONS AND DESCRIPTIONS

Distribution of the Luminous Organs

The luminous organs of *C. ritteri* are widely distributed over the body surface and some of the fins, though gradation is not uniform throughout the body. The organs are so numerous that their total number is difficult to estimate. Each organ is very small, 0.11–0.15 mm. in diameter, and is provided with a pigment sheath. In addition, these sink within the epidermis. Therefore, it is scarcely possible to observe the organs with the naked eye. However, they can be seen as small black spots under a low magnification.

In general, the densely distributed areas of luminous organs agree well with the jet-black color pattern marked on the body. The ground color of the head and body preserved in formalin is chocolate brown, but the tip and ventral surface of head are black, as is the belly. The first and second dorsal fins and the pectoral fin are edged with a white band. There are distinct black markings on the ventral surface of the

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upper eyelid, the base of the pectoral fin, the flank, and the ventroposterior corner of the caudal peduncle. These blackish areas are equipped with a greater number of luminous organs than are the other portions of the body. The most concentrated area of organs is the flank, which is dotted with black pigments (Fig. 1), the number of organs being 11–14 per square mm. On the other hand, the luminous organs are most sparse on the dorsal region of the body, excluding the head. On this area few luminous organs could be recognized.

Of particular interest is the presence of luminous organs studded on the ventral surface of the upper eyelid (Fig. 2). They are most conspicuous on both the anterior and posterior portions of the upper eyelid, but are poorly developed or absent at the central portion immediately above the eyeball.

Histological Features of the Luminous Organs

The epidermis of *C. ritteri*, in which the luminous organs are embedded, is composed of a stratified squamous epithelium with some mucous cells. This layer is lined with the stratum of dermis which consists of fibroelastic tissues (Fig. 3). Throughout the luminous area there extends a thin layer of pigment cells between the dermis and the epidermis, and the luminous organs are usually set on this pigment layer. On the scaled area the organs are found to be scattered among the placoid scales. Most of the luminous organs are obliquely situated and slightly inserted in the distal portion of the dermis.

Each luminous organ is a hemispherical cup in shape, and is composed of four main elements, (1) photogenic cells, (2) an irislike structure of pigment cells, (3) lens cells, and (4) a pigment sheath covering the organ.

The photogenic cells, approximately 7–12 in number, occupy the bottom of the organ. These cells are of a glandular type with an eosinophil secretion in their distal portion. Photogenesis seems to be intracellular. The lower half of a mass of photogenic cells is covered directly with the pigment sheath without a reflectorlike structure (Fig. 3).

Along the peripheral border of the mass of photogenic cells, there is a crowding of the pigment cells (Fig. 3). These are arranged in a circle and send out dendritic inward projections covering the cup. They apparently are capable of controlling themselves in the area which intercepts the photogenic body. This structure, therefore, may serve as an iris to regulate the amount of the light emitted from the photogenic cells. The arrangement of pigment cells of this structure resembles that of Etmopterus frontimaculatus rather than E. lucifer, described by Ohshima (1911: 4). The irislike structure of the latter species is more developed, that is, the pigment cells extend further toward the lens cells (Fig. 4).

Each luminous organ bears two or three lens cells lying above the cup. These cells are peculiar in containing a large amount of homogeneous concretion stained with orange G in cytoplasm, though some are vacuolated. This fine structure perhaps acts as a lens to concentrate the light emitted from the photogenic body. The nucleus, ovoid in shape, lies near the base of the cells. Because of the lack of young material, it was

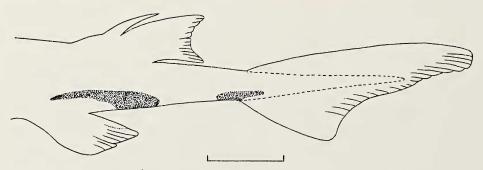


FIG. 1. Lateral aspect of posterior part of *Centroscyllium ritteri*, showing black markings on the flank and caudal peduncle in which luminous organs are densely distributed. Scale bar indicates 10 mm.

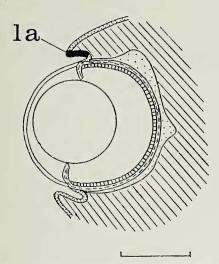


FIG. 2. Diagrammatic aspect of cross section through the eye, showing the supraorbital luminous area (la). Scale bar indicates 5 mm.

impossible to trace a sequence of development of the lens cells. The staining reaction of the lens cells in this species is quite dull as compared with that of *E. lucifer* (cf. Figs. 3, 4). This may be due to a poor condition of fixation.

The proximal border of the luminous organ is lined with the cup-shaped pigment sheath (Fig. 3), which may prevent the diffusion of light to the lining stratum. It continues to the iris at the distal end.

There is no reflectorlike structure at the base of the photogenic body, whereas highly developed luminous organs of teleostean fishes are usually provided with a well-developed reflector.

The histological examinations mentioned above show that the luminous organs of *C. ritteri* are not as well developed as those of *E. lucifer*, either in number or in structure. But as far as the structural evidence is concerned, it is not unreasonable to assume that these organs may be functional.

DISCUSSION

In the absence of living material, there is doubt as to whether or not the luminous organ of this shark is functional. Ohshima (1911: 7) and Schmidt (1931: 9), both working with living Etmopterus frontimaculatus, observed that feeble luminosity appears throughout the ventral surface and that the light is not produced

spontaneously but is emitted regularly by mechanical stimulation. The fact that the location and structure of the organs of *C. ritteri* are virtually the same as those of *Etmopterus* may imply that the present deep-sea shark is luminous. In his work on the luminous organs of elasmobranch fishes, Burckhardt (1900: 567–568) found luminous organs in both *Centroscyllium granulatum* and *C. fabricii*. Bigelow and Schroeder (1957: 38) also suggested the possibility of luminescence with thickenings of the black skin in some species of *Centroscyllium*. These data would lead one to suppose that all the members of *Centroscyllium* possess luminous organs, as is the case with the genus *Etmopterus*.

In several groups of fishes the characters of the luminous organs have been adequately discussed and appear to offer good evidence for separating the species. Haneda (1950: 216) and Matsubara (1953: 21) recognized two distinct species of the genus *Acropoma* based chiefly upon the form of the luminous organ, though the latter author added further features which enable us to distinguish the species. Iwai and Asano (1958: 8), upon studying the structure of the luminous organs as well as other

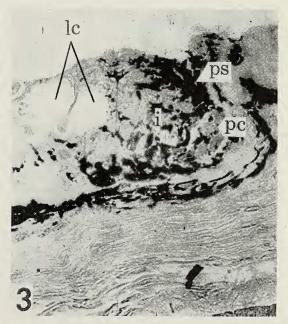


FIG. 3. Transverse section through a luminous organ on the flank of *C. ritteri*. (\times ca. 350). i, Iris; lc, lens cell; pc, photogenic cell; ps, pigment sheath.

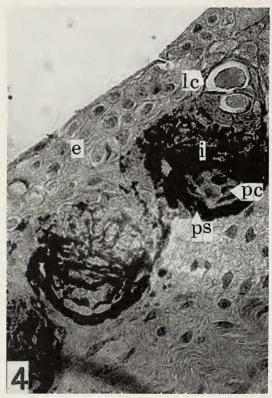


FIG. 4. Photomicrograph of section showing two luminous organs on the flank of *E. lucifer*. (\times *ca.* 350). ed, Epidermis; i, iris; lc, lens cell; pc, photogenic cell; ps, pigment sheath.

characteristics, concluded that Apogon marginatus should be a synonym of A. ellioti. In their key to the species of Etmopterus, Bigelow and Schroeder (1957: 61) utilized the black markings on the flank which include the heavily dotted pigment cells of the luminous organs. Judging from the results of the present study it seems likely that the distribution of luminous organs, especially those on the flank and caudal peduncle which form peculiar markings, serves as one of the specific characters of the genus Centroscyllium.

Attention should be called to the curious placement of luminous organs on the ventral surface of the upper eyelid. The situation of these organs is similar to the series *Li* of *Chauliodus sloani* Schneider described by Tchernavin (1953: 68). The latter consists of 4–6 cup-shaped organs situated within the fold of skin above the eye. The role of these organs is unknown, but

Tchernavin (1953: 68) suggested that such orbital photophores serve to illuminate approaching prey or to excite the eye.

SUMMARY

1. Centroscyllium ritteri Jordan and Fowler, like the other species of Centroscyllium or Etmopterus, is provided with a number of minute luminous organs on the body surface.

2. The densely distributed areas of luminous organs agree well with the jet-black color pattern marked on the body, especially those on the ventral surface of the upper eyelid, belly, and flank.

3. Each luminous organ is composed of the photogenic cells, an irislike structure of pigment cells, the lens cells, and a pigment sheath.

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